THE RECURRENCE OF TROPIDOLEPTUS CARINATUS IN THE CHEMUNG FAUNA OF VIRGINIA[1]

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For many years after the standard sections of the New York Devonian formations and their faunas had become well known, the brachiopod *Tropidoleptus carinatus* was supposed to be confined in its geologic range to the 1,100 or 1,200 feet of shale comprising the Hamilton formation in central New York. No trace of this fossil has ever been found in the typical Genesee and Portage faunas which follow the Hamilton fauna in west central New York. The entire absence of the species from the Genesee and western Portage faunas of New York seemed to indicate that the life of the species came to an end with the close of Hamilton sedimentation in central New York. But the discovery of *T. carinatus* in the Chemung of southern New York 2,000 feet above the top of the Hamilton by Professor H. S. Williams[2] several years ago proved that this species instead of becoming extinct at the close of the Hamilton had only changed its habitat. More recently Williams and Kindle[3] have found that *Tropidoleptus carinatus* and other well-known Hamilton species comprise the major part of the fauna at certain Chemung horizons in southern New York 2,000 feet or more above the top of the Hamilton formation. In this paper it will be shown that this and other Hamilton species reappear in the Chemung fauna of Virginia as they do in New York. The appearance of *T. carinatus* in the Chemung fauna of Virginia in abundance is especially notable because it is seldom found at the horizon of the Hamilton fauna so far to the southwest in this part of the Allegheny region as the occurrence in the rocks of Chemung time which will be described.

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[2] *Bull. U.S. Geol. Survey No. 3* (1884), 24.

[3] *Amer. Jour. Science*, XIII (1902), 427–30; *Bull. U.S. Geol. Survey No. 210* (1903), 90–91.

This recurrent Hamilton fauna was collected in Bath County, Virginia, near Mountain Grove post-office. The relationship which it bears to the other faunas which are known in the section from which it comes will be indicated by the following section of the rocks exposed along Little Creek at Mountain Grove post-office.

SECTION AT MOUNTAIN GROVE, VA.

	Feet
h. Thin-bedded, hard, gray sandstone and interbedded shale	700
g. Thin-bedded, hard, gray sandstone and interbedded shale	100
f. Rather hard, sandy, dark-blue shale and some thin bands of sandstone with Portage fauna	600±
e. Black, hard fissile shale	100
d. Covered	70
c. Hard, black, and dark greenish-gray calcareous shale	6
b. Black, blocky, tough shale	20
a. Dark, coarse, ferruginous sandstone with frequent concretions of pyrites (Oriskany)	20+

The sandstone at the base of the section holds the usual type of Oriskany fossils and clearly represents the Oriskany sandstone. The fauna of the lower 26 feet of calcareous and blocky shale is rather meager in this section as compared with the rich fauna often found at this horizon. The species collected from it are the following:

FAUNULE *c*, MOUNTAIN GROVE, VA.

Orbiculoidea lodiensis media	*a*
Anoplotheca acutiplicata	*c*
Conularia sp.	*r*

This faunule taken alone, of course, could hardly be cited as satisfactory evidence of a definite horizon. An extended study[1] of the fauna found at this horizon by the writer throughout an extensive region in the Allegheny Mountains has shown, however, that the horizon is that of the Onondaga limestone. The greater part of the Hamilton horizon is covered in the section.

The next higher fauna which was collected from this section is shown in the following list of species from the lowest beds in the sandy shales marked *f* in the section outcropping at Cash's store.

[1] *The Onondaga Fauna of the Allegheny Region*, Bull. U.S. Geol. Survey (in press).

FAUNULE *f*, MOUNTAIN GROVE, VA.

Ontaria suborbicularis
Paracardium doris
Styliolina fissurella
Bactrites aciculum
Orthoceras sp.
Probloceras cf. lutheri
Tornoceras uniangulare

The student familiar with the western Portage or *Buchiola retrostriata*[1] fauna will at once recognize in this faunule a representative of that fauna. Its occurrence at a definite horizon in Virginia and Pennsylvania has been previously noted by the author.[2] Clarke[3] and Swartz[4] have recognized the same fauna in western Maryland. It should be noted here that the *Buchiola retrostriata* (*G. speciosa*) fauna listed by the author from the White Sulphur Springs, Virginia,[5] section is not the faunal equivalent of the *B. retrostriata* (*G. speciosa*) fauna of Williams,[6] but comprises only the upper portion of Williams' fauna. As the term is used by Professor Williams in Bulletin 244 it includes at least three distinct faunas, each of which has a fairly definite position in the sections. The writer's past and present usage makes it include only the latest of these three—the Portage—thus making it synonymous with the western Portage or Naples fauna of New York. The recorded range of this species makes it permissible to use the name in Professor Williams' comprehensive manner if it is desirable to consider these several faunas collectively. But the writer prefers the more restricted usage adopted by Professor Williams in an earlier paper,[7] according to which it includes only the western phase of the Portage fauna. The Portage fauna appears to characterize about 600 feet of the Mountain Grove section. Although the section is mostly exposed and the order of succession of the different parts is clear, the local buckling of

[1] This fauna has also been called the *Manticoceras intumescence* fauna and Naples fauna in New York.

[2] *Bull. U.S. Geol. Survey No. 244* (1905), 35, 40–41; *Jour. Geology*, XIV (1906), 633.

[3] *N.Y. State Mus. Mem. 6* (1904), 212.

[4] *Jour. Geology*, XVI (1908), 340.

[5] *Bull. U.S. Geol. Survey No. 244* (1905), 35.

[6] *Ibid.*, 51.

[7] *Bull. U.S. Geol. Survey No. 210* (1903), 115.

some of the softer beds leaves some uncertainty regarding the exact thickness of the section.

It is with the next fauna in the section that this paper is chiefly concerned. This fauna appears after the bluish-gray sandy shales and very thin sandstones have given place to very hard thin-bedded sandstones as the dominant lithologic characteristic of the section. In beds of this kind in division *g* of the section occurs the first appearance of the Chemung fauna. The following is a list of the species collected from this horizon:

FAUNULE *g*, MOUNTAIN GROVE, VA.

Productella sp.	*c*
Camarotoechia cf. congregata	*c*
Leiorhynchus sp.	*c*
Atrypa spinosa	*c*
Rhipidomella impressa	*r*
Rhipidomella cf. penelope	*r*
Schizophoria tioga	*c*
Ambocoelia umbonata	*c*
Schuchertella chemungensis	*r*
Delthyris mesacostalis	*c*
Spirifer medialis	*c*
Reticularia fimbriata	*r*
Tropidoleptus carinatus	*a*
Mytilarca chemungensis	*r*
Modiomorpha sp.	*r*
Nuculites cf. oblongatus	*r*
Cyclonema sp.	

The stratigraphic position of this fauna several hundred feet above a typical Portage fauna shows plainly that it lies far above the Hamilton horizon. Its association with *Schizophoria tioga* and *Mytilarca chemungensis* indicates that it is here associated with a Chemung fauna. In the next division of the section above this we find *Spirifer disjunctus* and other well-known Chemung fossils as shown in the following list from division *h* of the section:

FAUNULE *h*, MOUNTAIN GROVE, VA.

Aulopora sp.	*r*
Chonetes scitula	*c*
Productella hirsuta	*c*

Atrypa spinosa	*c*
Stropheodonta (Douvillana) mucronatus	*a*
Stropheodonta perplana var. nervosa	*r*
Schizophoria tioga	*c*
Rhipidomella sp.	*r*
Camarotoechia sp.	*r*
Spirifer disjunctus	*c*
Edmondia sp.	*r*
Schizodus rhombeus	*r*
Sphenotus contractus	*c*
Loxonema sp.	*r*

The case of recurrence which has been cited involves a somewhat different phase of the phenomenon from that represented in the New York occurrences of *T. carinatus* in the Chemung.

The presence of a recurrent Hamilton species like *Tropidoleptus carinatus* in the Chemung fauna of southern New York involves its withdrawal from at least the major part of the New York area at the end of Hamilton sedimentation to some part of the sea furnishing a more congenial environment than that which accompanied Genesee and Portage sedimentation. In the newly adopted habitat or in a small portion of the old one it found a haven where those conditions of the Hamilton sea which were essential to its life were maintained throughout Genesee and Portage time. With the initiation of Chemung sedimentation *T. carinatus* extended its habitat back again over a part of the area which it had previously occupied.

The case of recurrence which I have given in Virginia does not involve, as in New York, a retreat of the species before unfavorable conditions at the close of the Hamilton and later recovery of lost territory, since it apparently never occupied this territory in Hamilton time. It represents instead the acquisition of a new habitat which had been outside the limits of its geographical range in the Hamilton sea. The writer's study of the Devonian faunas in the Allegheny region indicates that the typical Hamilton fauna with *T. carinatus* does not extend as far to the southwest as Mountain Grove, although the Hamilton sea extended much beyond that point to the southwest. The occurrence of a Hamilton species in abundance in the Chemung fauna of this part of Virginia thus

seems to indicate that the marine biotic conditions of the New York Hamilton and the Virginia Chemung seas were more nearly alike than they were in different parts of the same sea in the two states during Hamilton sedimentation.

A matter of some interest and importance in connection with the recurrence of this species and its associates relates to the location of its Portage habitat, or place of retreat between the close of Hamilton and the beginning of Chemung sedimentation. It has been shown by Prosser[1] and others[2] that in eastern New York the Hamilton fauna including *Tropidoleptus carinatus* continued in a slightly modified form to live on during Portage time. In other words, this species and some of its allies at the close of Hamilton time became extinct in central and western New York but survived in a narrow belt along the eastern margin of their old habitat and continued to live near the eastern shore of the Appalachian Gulf throughout Genesee and Portage time. (See Fig. 1.)

In Pennsylvania the writer's work has shown that the Ithaca and Portage faunas bear the same geographic and stratigraphic relations to each other that they do in New York. In western Pennsylvania the Portage formation is characterized by a typical western Portage or Naples fauna.[3] On the Susquehanna River an Ithaca fauna occupies the same horizon which is held by the Portage fauna in the Altoona section.[4] East of the Susquehanna River 35 miles, at Pine Grove, the writer has recently collected a faunule of the Ithaca fauna which shows a more prominent Hamilton element than the fauna exhibits at the Susquehanna River. It includes *Tropidoleptus carinatus*, as will be seen from the following list of its species:

[1] "The Classification and Distribution of the Hamilton and Chemung Series of Central and Eastern New York," *Fifteenth Ann. Rep. State Geol. New York* (1897), 208–14.

[2] H. S. Williams, "The Correlation of Geological Faunas," *Bull. U.S. Geol. Survey No. 210* (1903), 71–72; John M. Clarke, "The Ithaca Fauna of Central New York," *Bull. N.Y. State Mus. No. 82* (1905), 53–65.

[3] E. M. Kindle, "Faunas of the Devonian Section near Altoona, Pennsylvania," *Jour. Geology*, XIV (1906), 633.

[4] H. S. Williams and E. M. Kindle, "Contributions to Devonian Paleontology, 1903," *Bull. U.S. Geol. Survey No. 244* (1905), 69–92.

ITHACA FAUNA AT PINE GROVE, PENNSYLVANIA

Aulopora sp.	*r*
Cystodictya meeki	*c*
Chonetes scitula	*a*
Spirifer pennatus var. posterus	*a*
Tropidoleptus carinatus	*c*
Palaeoneilo plana	*c*
Modiomorpha cf. subalata	*r*
Goniophora minor	*r*
Paracyclas liratus	*r*
Actinopteria peristralis	*c*
Coleolus aciculum	*r*
Pleurotomaria capillaria	*r*
Pleurotomaria sulcomarginata	*c*
Murchisonia cf. leda	*r*

From central and eastern Pennsylvania the Ithaca fauna extends southward across Maryland far into Virginia. The Portage and Ithaca faunas occupy the same relative stratigraphic and geographic positions in this southerly area[1] as in New York state, the former having its maximum development to the westward of and parallel with the Ithaca fauna. Evidence that *Tropidoleptus carinatus* lived during Portage time near the eastern margin of the Appalachian Sea in Virginia as well as in Pennsylvania and New York is furnished by a collection representing the Ithaca fauna which the writer made at Bells Valley, Virginia. In this collection *T. carinatus* is a very abundant species, while another pre-Portage species, *Rhipidomella vanuxemi*, occurs sparingly with it.

The relation which *Tropidoleptus carinatus* bears to Hamilton, Portage, and Chemung sediments may be illustrated by the accompanying diagram which shows the easterly restriction of the species in New York during Portage time and the westerly extension of its habitat during Chemung time. The easterly or coastwise restriction of the species at the close of the Hamilton could be graphically shown for Pennsylvania and Maryland by diagrams of similar character, except that the Tully limestone would be omitted.

[1] E. M. Kindle, *Bull. U.S. Geol. Survey No. 244* (1905), 35, 41, faunules 1380*B* and 1382*D*; Charles K. Swartz, *Jour. Geology*, XVI (1908), 328–46.

When it is recalled that the geographic range of this species in the eastern United States during the Hamilton extended from the Hudson River and the eastern part of the Allegheny Mountains to Michigan, Indiana, and southwestern Illinois, it will be seen that its east-west distribution was reduced during Portage time to a very small fraction of that which it enjoyed during Hamilton time. Our present knowledge of its occurrence in the Chemung indicates that only a very small part of its east-west Hamilton range was regained during the Chemung. The north-south distribution of the species in the Allegheny region did not, however,

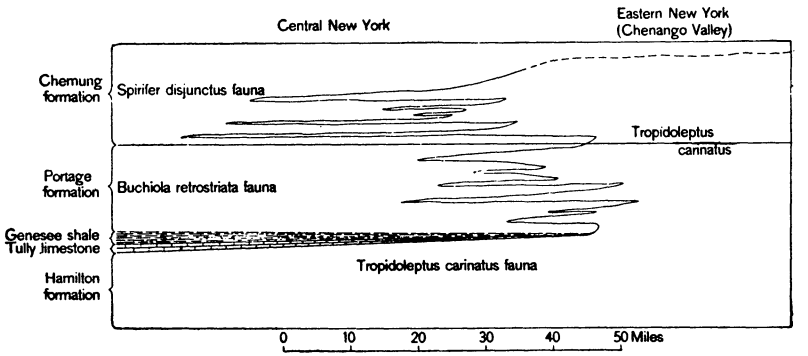

FIG. 1.—A diagrammatic east-west cross-section of the Middle and Upper Devonian of southern New York showing the relations of *Tropidoleptus carinatus* to the western faunas during Portage and Chemung time. Total thickness of the section is about 2,700 feet.

differ greatly during the Portage and Chemung epochs from what it had been during the Hamilton. In this direction it appears to have extended its range slightly in Chemung time beyond what it had been during Hamilton time. During Portage time the species was confined to a sublittoral belt, narrow but long, which reached south into Virginia along the eastern shore of the Appalachian sea. From the limits of this coastwise belt of the sea the more favorable conditions of environment which accompanied the initiation of Chemung sedimentation encouraged the migration of its colonies westward into the areas where we now find them in the Chemung of New York and Virginia. These colonies

appear to have experienced a succession of alternate extensions and withdrawals in the New York Chemung.

It is essential to a clear understanding of the interrelationship of these distinct but contemporaneous faunas to recognize the fact that zoölogical provinces were often as distinct in the Paleozoic seas as in those of the present. In the Devonian we know that there were such provinces, but as yet we know but little of their limits in any given epoch. We also know comparatively little about the factors which set the limits to faunal provinces. It is safe to conclude, however, that the recurrence of a fauna has been due to the oscillation or migration of the factors which conditioned its geographical distribution. Attention has been called to one of these factors by Ulrich[1] in discussing the recurrence of a Spergen fauna in the Ste. Genevieve limestone. He conceives one of the conditions inducing the recurrence of this fauna to have been "the subsidence or modification of barriers allowing communication with seas more permanently inhabitated by the invading fauna." The probable combination of two factors which are no doubt often effective in controlling recurrence is cited by Bagg in discussing the recurrence of a Cretaceous brachiopod in the Eocene of Maryland. Bagg[2] believes this case of recurrence to have been due to a deepening of the sea south of New Jersey, assisted perhaps by cold currents from the north which killed off the other Cretaceous species and encouraged the southward migration of a shell which previously had lived in the New Jersey region.

While the development or removal of land barriers and changes in the character of sediment have doubtless been at times influential in causing the recurrence of faunas, it is probable that changes in the temperature of marine waters have much more frequently been the direct effective agency in causing recurrence. Among the agencies controlling faunal distribution it is most probable that temperature has in the past, as in the present, been a factor of paramount importance. The recurrence of a species necessarily represents the recurrence of those factors in its environment which

[1] *Prof. Paper U.S. Geol. Survey No. 36* (1905), 49.

[2] *Am. Geologist*, XXII (1898), 272–373.

have throughout its life history controlled its distribution. Recurrent faunas, therefore, afford special opportunities to discover the factor most essential to the life of the fauna in a given case through elimination of those factors which are common to the sediments from which it is absent and in which it makes its earlier and later appearances. With reference to the sediments, the recurrence of a species after long absence from the section thus affords evidence of similar conditions having been present in widely separated formations, the importance and significance of which might otherwise not have been apparent.

In the light of these general considerations we may inquire into the cause of the eastward retreat of the species which has been shown to have occurred at the beginning of Genesee sedimentation and its later westward and southwestward migration. The evidence of such a movement has been cited on a preceding page. The close of Hamilton sedimentation is marked in western New York by a great change in the character of the sediments. The sandy and often calcareous shales of the Hamilton are succeeded by the thin band of the Tally limestone and the fissile black carbonaceous shales of the Genesee in the central and western parts of the state (see Fig. 1). When these black Genesee and the succeeding lighter-colored shales of the Portage are not entirely barren they are occupied by a fauna of "evident deep-water habit having nothing in common with the preceding Hamilton fauna."[1] These black shale sediments following the Hamilton extend southward beyond the Potomac River. This sharp contrast between the sediments and faunas of the Hamilton and those of the Genesee shales includes the total disappearance of the large coral fauna of the Hamilton. The annihilation at the close of the Hamilton of all fossils which, like corals, require shallow waters, and the shifting of those species which survived to the comparatively shallow coastwise waters points plainly to the deepening of the sea at the close of Hamilton time. Much additional evidence for the deep-sea conditions which prevailed during Genesee and Portage time in western New York

[1] John M. Clarke, "The Naples Fauna in Western New York," *N.Y. State Mus. Mem. No. 6* (1904), 211.

has been given by Dr. John M. Clarke[1] and requires no restatement here. A lower temperature of the water doubtless accompanied the deepening of the sea during early Genesee time and was probably the chief immediate cause of the complete disappearance of the shallow water fauna of the Hamilton from a large part of the Devonian sea with the appearance of the pelagic Genesee fauna. The sea became shallow again during Chemung time. This is shown by the ripple-marked sandstones which may be seen in Chemung sediments from New York to southern Virginia. That the remnant of the Hamilton fauna which had survived till Chemung time in the shallow coastwise waters in the eastern margin of the Devonian sea found in the Chemung sea a temperature similar to that of the old Hamilton sea is attested by such colonies as the one which has been described from Virginia.

The distribution of *Tropidoleptus carinatus* in the Chemung sediments as detached, often widely separated, colonies is in some degree comparable with that of *Ostrea virginica* along the present Atlantic coast. This warm-water species is unknown along wide stretches of the northern New England coast but in the Gulf of St. Lawrence flourishes in waters, which in their deeper parts afford a habitat for such Arctic forms as *Mya truncata*. That a low temperature is as essential to the life of the latter as is a high temperature to the former is illustrated by the fact that while in the Gulf of St. Lawrence *M. truncata* is found in the deeper waters only, in Greenland waters it is said to be sufficiently common at low water to furnish food for the Arctic fox and other land animals.[2] The character of the geographical conditions which permit representatives of the south Atlantic and north Atlantic coast faunas to live on adjacent parts of the sea bottom is indicated in the following quotation from Doctor MacBride.

> The whole north coast of Prince Edward Island is fringed by a series of parallel sand-bars, and it is owing to this circumstance that the oyster is able to flourish there. All who know the coast of the Gulf of St. Lawrence are aware that the water even in summer is very cold; so cold indeed that though

[1] *Op. cit.*

[2] J. F. Whiteaves, *Catalogue of the Marine Invertebra of Eastern Canada* (Geol. Surv. of Canada, 1901), 148.

the adult oyster could live in it, it could not reproduce itself, for the larvae would perish. But as the Gulf water flows over the sand-bars and shoals alluded to, it becomes heated up by the summer sun, and reaches a temperature which permits, in favorable years at least, of successful spawning. Oysters are accordingly confined to such places on the coast of Canada as present conditions similar to those mentioned above. They exist in the Baie de Chaleur, in some of the shallower inlets on the New Brunswick coast, at a few points on both shores of Prince Edward Island, and on the Northern Coast of Nova Scotia. In every case, however, we have to do with isolated colonies inhabiting warm spots surrounded by a great belt of cold water, so that although the larvae could be carried to great distances in the fortnight of their free-swimming life, they are all killed off by the cold.[1]

Protecting bars may at times have been a factor in modifying the temperature of the Devonian sea where Portage and Chemung colonies of *T. carinatus* gained a foothold, as they are now in sheltering the oyster at Prince Edward Island. But there can be no doubt that all times during the upper Devonian the eastern or coastwise belt of the Appalachian gulf was shallower than its more pelagic portion. Its waters must also have been comparatively warm, at least during the spawning season of its molluscan fauna. Since *Tropidoleptus carinatus* is confined in the late Devonian to the sediments of this belt of comparatively shallow sea, and consequently warmer water, we must conclude that its restriction and late survival here was due primarily to the higher average temperature of this part of the Devonian sea.

[1] E. W. MacBride, "The Canadian Oyster," *Canadian Rec. of Sci.*, IX (1905), 154–55.